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RELATED FORMS

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By P. M. DAVID

(National Institute of Oceanography)

INTRODUCTION

THE material used in the investigations recorded here was taken from the collections made by vessels of the Discovery Committee and, later, of the National Institute of Oceanography.

The bulk of these collections comes from the Southern Ocean, mainly from Antarctic waters, but a considerable quantity of material has been accumulated over the years from tropical and subtropical regions as well.

These more northerly collections while perhaps not enough to permit exhaustive studies of the life histories and distribution of single species of planktonic animals nevertheless contain much that is useful for the systematic work so necessary as a first step towards the ecological and distributional studies that might be possible when larger collections have been made in warmer seas.

This paper is an attempt to explain some anomalies of distribution of an apparently valid and homogeneous species, relatively well represented in the collections, which on careful examination appears to be a group of three forms, each, in the present state of knowledge, being entitled to specific rank.

Sagitta planctonis was described by Steinhaus (1896) from material taken in shallow net hauls off S.W. Africa. In 1905 Fowler described a new species *S. zetesios* taken by H.M.S. "Research" in deep water in the Bay of Biscay. These two species were combined into one by Ritter-Zahony in 1911 under the name *S. planctonis*. Although this arrangement has remained to the present day, it has been suggested both on anatomical grounds (Tokioka, 1939; George, 1952) and on distributional grounds (Moore, 1949) that two distinct forms are combined as one species.

Probably the most certain anatomical feature for specific determination of chaetognaths is the shape and position of the seminal vesicles. Unfortunately mature specimens of many species of chaetognaths are but rarely caught and *S. planctonis* is exceptionally uncommon in the fully mature state. It is for this reason that Ritter-Zahony's figure and description of the mature vesicles of this species, has of necessity been accepted by subsequent authors, despite the fact that Tokioka (1939) and George (1953) have figured *S. planctonis* with vesicles or remnants of the vesicles differently situated.

Specimens which appear to be *S. planctonis*, with seminal vesicles as described and figured by Ritter-Zahony (1911), are common in the Antarctic plankton samples of the "Discovery" Collections, and are distributed from the surface to 1500 m. Besides these, there are specimens from tropical and subtropical hauls from deep

water which agree with Ritter-Zahony's table (1911, p. 30, "90 specimens from the Atlantic Ocean"), but which have not been found with intact seminal vesicles. Traces of these structures however have been seen which appeared to be differently situated from those figured by Ritter-Zahony (1911, fig. 36). Moreover although the distribution of *S. planctonis* is well established as mesoplanktonic, specimens apparently of the same species (i.e. within the range of variation given, or implied, by Ritter-Zahony) have been taken in shallow hauls in the subtropics, associated with typically epipelagic forms, and often in too large numbers for this anomalous distribution to be ascribed to some freak of distribution of the mesoplankton.

Thus, from distributional evidence it seemed that there were at least two separate species in the collections grouped under one name, an opinion held for many years by Mr. J. W. S. Marr (personal communication). In the absence of any established anatomical differences this opinion remained conjectural.

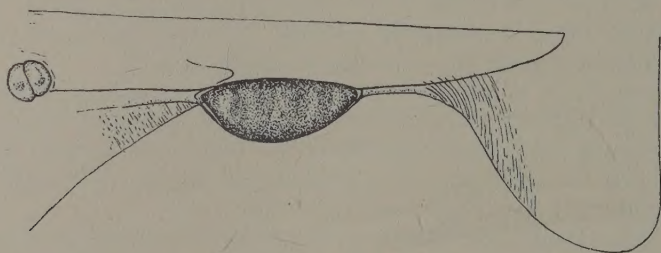


FIG. 1.—Seminal vesicle of *S. planctonis*.

Recently Mr. A. de C. Baker (also working on the "Discovery" collections) noticed, and drew my attention to, a large mature chaetognath in perfect condition (Pl. Ia) which was taken at Stn. 1685 ($41^{\circ} 21.8' S.$, $148^{\circ} 51' E.$ 15.ii.36) to the East of Tasmania between 1000 and 750 m. Although the seminal vesicles (see Text-fig. 1) of this specimen were not in agreement with Ritter-Zahony's figure the specimen was in other respects identical with the subtropical forms referred to as *S. planctonis*. The Tasman sea is an area where *S. planctonis* is found in the surface waters as it is off Bermuda (Moore, 1949), S.W. Africa (Steinhaus, 1896), in the Agulhas current, off N.E. New Zealand and in parts of the North Atlantic ("Discovery" collections). I therefore supposed at first that this surface form of warmer latitudes was *S. planctonis* Steinhaus and that the specimen from Stn. 1685 was breeding in deep water as do certain other surface forms, e.g. *S. lyra* and *S. gazellae* (Ramault and Rose, 1946; Ghirardelli, 1950; David, 1955) and that the Antarctic form was the same as the cosmopolitan deep-water *S. planctonis* of Ritter-Zahony and others, and probably referable to *S. zetesios* Fowler. Examination of a number of deep living specimens from tropical and subtropical waters however, showed that while they resemble the surface form closely they are quite different from the Antarctic form.

I have therefore concluded that grouped under the one name *S. planctonis* there are three distinct species, easily distinguishable when fully mature, but closely

similar in the immature stages. These are (a) the surface living form of tropical and subtropical waters, originally named *S. planctonis* by Steinhaus, (b) the deep water form also of warm latitudes named *S. zetesios* by Fowler, and (c) the Antarctic form described as *S. planctonis* by Ritter-Zahony, occurring from near the surface down to 1500 m. or more. I propose to return to the original nomenclature for the two tropical and subtropical forms, calling them (a) *S. planctonis* Steinhaus and (b) *S. zetesios* Fowler. The Antarctic form I propose to name *S. marri* after Mr. J. W. S. Marr.

SYNONYMY AND DESCRIPTION OF SPECIES

Examination of the literature shows that whereas Ritter-Zahony had recognized the Antarctic form as differing both in size at maturity and in the numbers of teeth from the "typical" deep living *planctonis*, he had not considered that any significant difference existed between *S. planctonis* Steinhaus and *S. zetesios* Fowler. This was due partly to the inadequate description of *S. planctonis* Steinhaus and partly to the absence of the species from the Gauss collections. Also, setting aside the distributional differences, the only obvious feature distinguishing *S. planctonis* from *S. zetesios* was the greater number of posterior teeth in the latter species, the Antarctic form in this respect being intermediate and apparently bridging the gap between *S. planctonis* and *S. zetesios*. It was hardly surprising that Ritter-Zahony regarded the three forms as variation (and not great variation) in one species. However the present evidence of the mature vesicles of *S. planctonis* and *S. marri* immediately separates them into two species and thus invalidates the intermediate nature of the Antarctic form *S. marri*. The difference between *S. planctonis* Steinhaus and *S. zetesios* Fowler is once again dependent upon the number of posterior teeth, and previous records show this to be consistent. Fowler (1905 and 1906) records six specimens of *S. planctonis* none of which had more than 12 posterior teeth. Michael (1911) records *S. planktonis* with up to 12 posterior teeth. Tokioka (1940) does not record more than 12 posterior teeth in specimens from the Tasman sea, and this is confirmed by Thomson (1947) from the same area, although in two size groups (see Text-fig. 2) he records up to 13 posterior teeth.

Records of *S. zetesios* are more frequent and all show a much higher maximum. For example, Fowler (1905, 1906) gives up to 19 posterior teeth, Michael (1911, 1919) up to 19, Ritter-Zahony (1911) up to 22, Burfield and Harvey (1926) up to 19, and Burfield (1930) up to 19. Some of these previous records are summarized in Text-fig. 2.

Published information on the shape and position of the seminal vesicles is conflicting. Fig. 1 in Steinhaus' paper shows no seminal vesicles despite the quite advanced ovaries. Fowler (1905) figures the vesicles of *S. zetesios* nearer the posterior fins than the tail. He shows them in the same position in the figures in the Siboga report (1906), pointing out that the seminal vesicles were only projecting slightly.

Michael (1911) shows *S. planktonis* with conical vesicles close to the tail fin, but his figure bears little resemblance to the mature vesicles of the Antarctic form, and none at all to the other forms. Ritter-Zahony (1911) figures the vesicles of the Antarctic

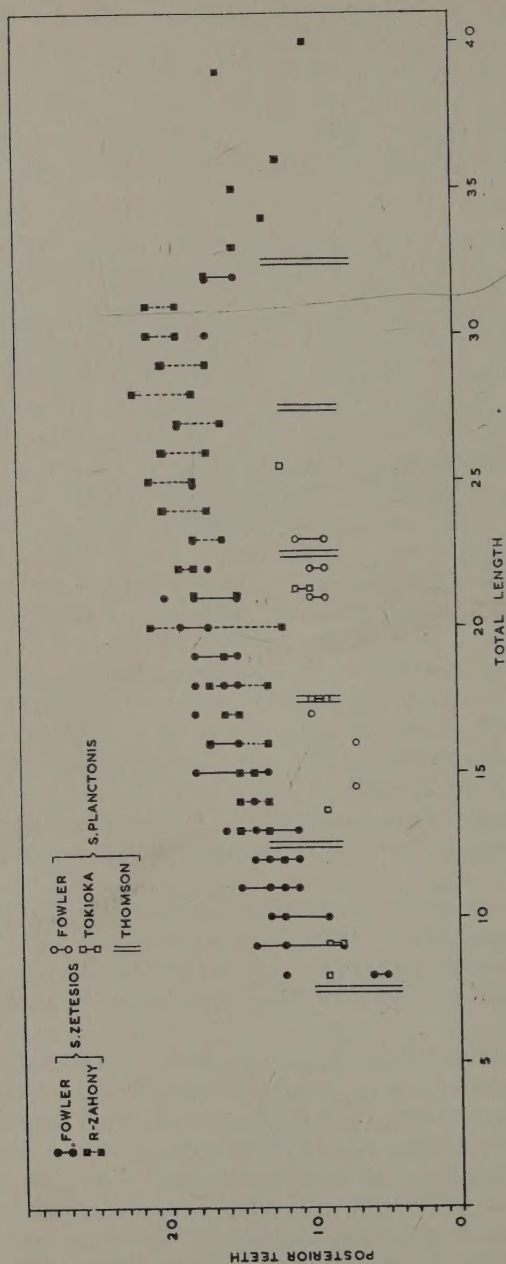


Fig. 2.—Numbers of posterior teeth plotted against body length for *S. planctonis* and *S. zetesios*.
Data from previous authors.

form as conical and in contact with the caudal fin. This has been subsequently regarded as the typical *planctonis* vesicle.

The figures in Germain and Joubin (1916) are of little help; they show *S. planctonis* with an evidently stylized vesicle in contact with both the posterior and caudal fins.

Tokioka (1939) figures the remnants of the vesicle in contact with the posterior fins—with Ritter-Zahony's figure alongside for comparison—and in his paper on the New South Wales plankton (1940) shows the rudiments of a vesicle in contact with the posterior fin.

Thomson (1947) did not figure *S. planctonis*, but in his key described the seminal vesicle as not in contact with either the posterior or caudal fins and said it "approaches the tail fin".

Fraser (1952) said the vesicles of this species were elongated and conical near the tail fin, but his photograph shows their remnants to be near to the posterior fins.

George (1952) gives the position of the seminal vesicles as in contact with the posterior fin, but the figure given in his paper does not show any detail of the shape of the vesicles. The largest specimen recorded in his table (p. 663) is 13.0 mm., and the size range for the species given in his table of diagnostic features (opposite p. 680) is from 12–20 mm. I have not seen either *S. planctonis* or *S. zetesios* with even rudimentary vesicles at this size, nor have I seen any specimens with confluent fins as shown in his fig. 13. It is possible therefore that he is dealing with another form altogether.

S. planctonis and related forms (as a group) are easily recognized by their robust form and extensive collarette and resemble each other so closely in appearance when immature that although authors have found certain characters which did not altogether agree with Ritter-Zahony's classic description, they felt sure on other grounds of the identity of their specimens and did not attempt to distinguish them further.

Some authors have employed the name *planctonis* spelt with a "k" instead of *planctonis* with a "c" as used by Steinhaus. Although the use of "k" instead of "c" is more properly derived the first published orthography *planctonis* must stand.

Sagitta planctonis Steinhaus, 1896

(Pl. IIa, fig. 3a)

Sagitta planctonis Steinhaus, O., 1896, Inaug. Diss. Kiel., pp. 1–49.

Sagitta planctonis Fowler, 1905; Fowler, 1906; Ritter-Zahony, 1909 (?); Tokioka, 1940; Thomson, 1947; Moore, 1949.

Sagitta planktonis Michael, 1911.

CHARACTERS:

Anterior fin rayless at the anterior end and along the inner edge: begins at the ventral ganglion. Length 24–32% of body length.

Posterior fin sharply triangular, apex of fin level with or slightly behind tail septum.

Tail stout, 19.2–21.4% of body length.

Anterior teeth up to 9, usually 6-8.

Posterior teeth up to 14, usually 10-12.

Hooks up to 11, usually 8-11.

Seminal vesicles elongate, in contact with posterior fins, simple, of the "*bedoti*" type. (see Text-fig. 1).

Ovaries completely filling body cavity when fully mature.

Collarette very prominent, extending to the tail in fully grown specimens.

Corona commences at the posterior end of the head and extends to about half way between the head and ventral ganglion. (see Tokioka 1940, fig. 86B).

Length up to 37 mm.

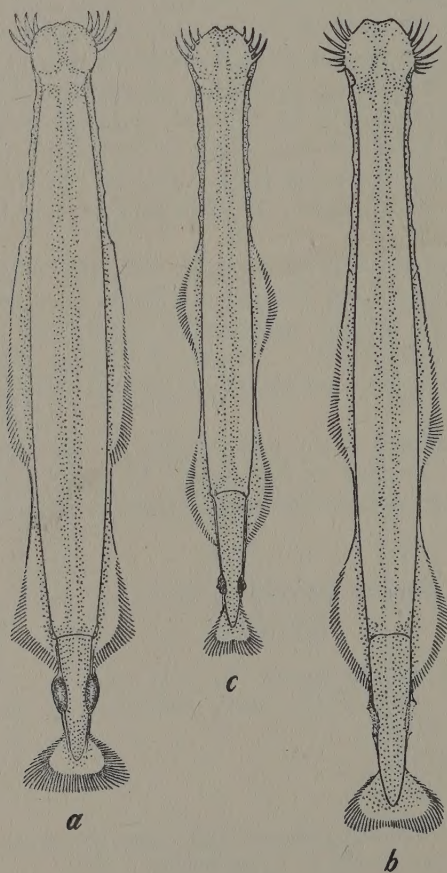


FIG. 3.—A comparison of the fin shape and position of the seminal vesicles. (a) *S. planctonis*, 37 mm. long. (b) *S. zelesios*, 38 mm. long. (c) *S. marri*, 28 mm. long.

Distribution. Bermuda, S.E. Africa, (Aghulas current area), Tasman Sea, off N.E. New Zealand, and parts of N. Atlantic. A surface living form breeding at a moderate depth (1000–750 m.).

Sagitta zetesios Fowler, 1905

(Fig. 3b)

Sagitta zetesios Fowler, G. H., 1905, Trans. Linn. Soc. Lond. (Zool.) Ser. 2 X, pp. 55–87.

Sagitta zetesios Fowler, 1906; Michael, 1911.

Sagitta planctonis (non Steinhaus) Ritter-Zahony, 1911 (part); Germain and Joubin, 1916; Michael, (1919); Burfield and Harvey, 1926; Burfield, 1930 (part); Bollman, 1934 (part); Kuhl, 1938 (part); Thiel, 1938 (part); Kramp, 1939 (?); Tokioka, 1939; Fraser, 1952.

Sagitta planktonis (non Steinhaus) Kramp, 1918 (?); George, 1952. (?)

CHARACTERS :

Anterior fin rayless or very sparsely rayed at the anterior end, beginning at or about the ventral ganglion. Length 20–26% of body length.

Posterior fin triangular, apex of fin level with tail septum.

Tail stout, 20–23% of body length.

Anterior teeth up to 12, usually 8–10.

Posterior teeth up to 22, usually 15–19.

Hooks up to 11, usually 8–10.

Seminal vesicles shape not known, but remnants of vesicle indicate that it is in contact with the posterior fin, elongate and of similar dimensions to those of *S. planctonis*.

Ovaries longest observed reached to half-way between the head and ventral ganglion.

Collarette very prominent, extending on to the tail in large specimens.

Corona similar to *S. planctonis*. See Ritter-Zahony 1911, fig. 35a.

Length up to 40 mm.

Distribution. A deep living form found in most deep oceans, but absent from the Antarctic.

Sagitta marri nov. sp. (Pl. IIb, fig. 3c)

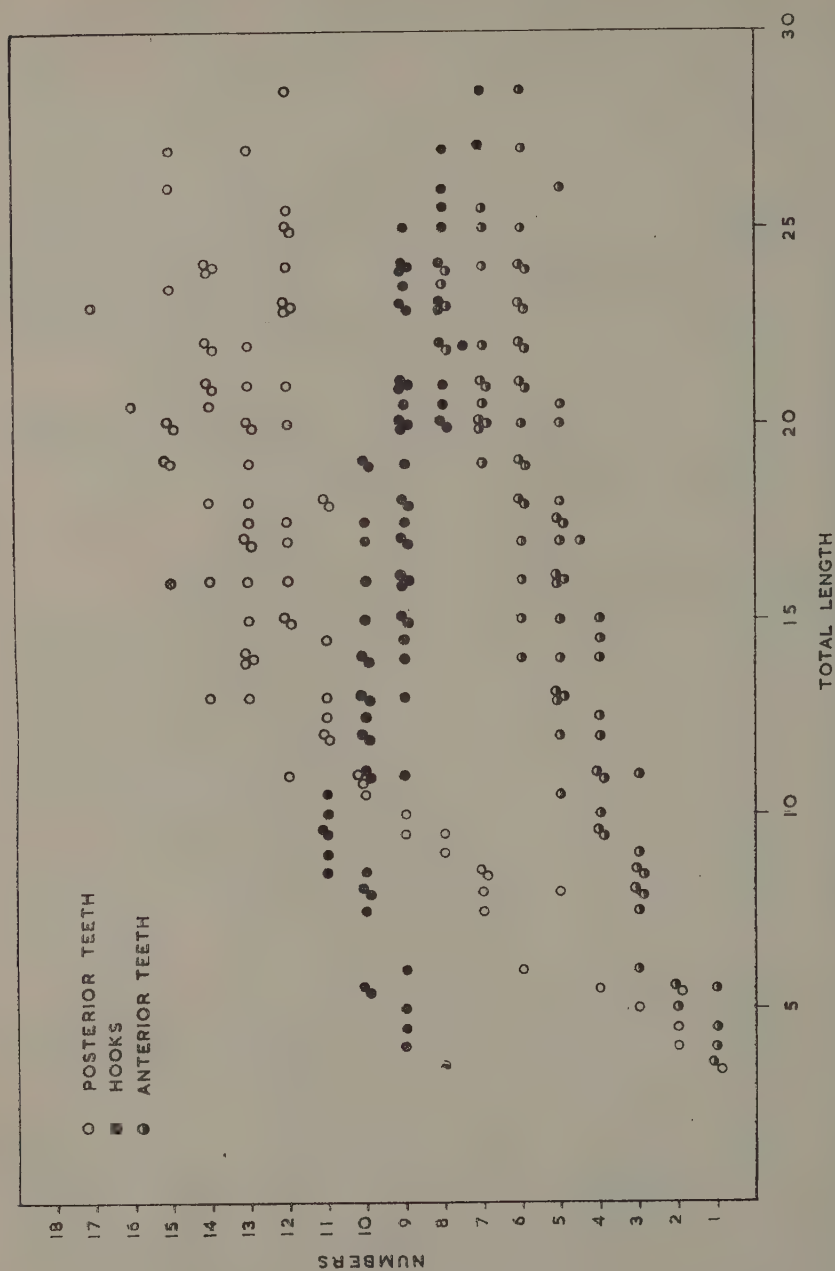
Sagitta zetesios Fowler, 1907 (*nec* Fowler 1905).

Sagitta planctonis (non Steinhaus) Ritter-Zahony, 1911 (part); Jameson, 1913; Johnston and Taylor, 1921; Burfield, 1930 (part); Bollman, 1934 (part); Mackintosh, 1937 (part); Thiel, 1938 (part).

Sagitta planktonis (non Steinhaus) Hardy and Gunther, 1936.

Holotype a mature specimen 23.9 mm. in length taken in a 70 cm. vertical closing net which fished between 750 and 500 m., at "Discovery" station 859: 59° 19.1' S., 68° 51.8' E.: 25.iv.32.

Body proportions: Total length 23.9 mm. (24.5 mm. including caudal fin); Tail segment 5.3 mm., 22.2% of total length; anterior fins 3.7 mm., 15.5% of total length.

Fig. 4.—Head armature numbers plotted against body length for *S. marri*.

Head armature : Hooks 6 and 8 ; anterior teeth 6 and 7 ; posterior teeth 16 and 16.

Gonads : Ovaries 7.2 mm., 33.2% of total length ; one fully mature seminal vesicle present, the other full-sized but not full of sperms.

Paratypes : 32 specimens taken in a 1 m. closing net fished from 700–400 m. at "Discovery" station 1782 : 58° 44.6' S.; 00° 00.7' E.; 3.vi.36.

The range of variation given below is that of the 76 specimens shown in Text-fig. 4.

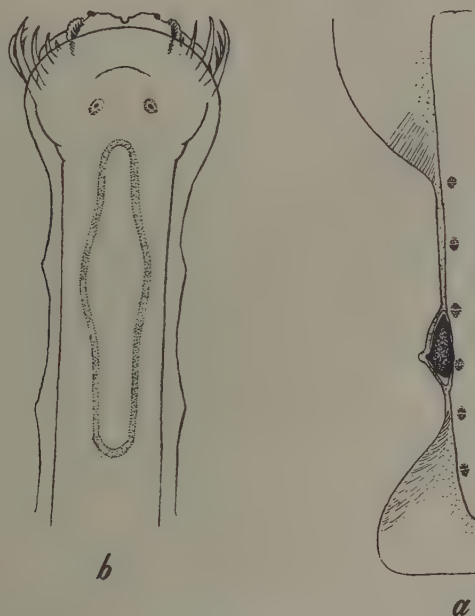


FIG. 5.—*S. marri*. (a) Shape and position of seminal vesicle. (b) Shape and position of corona.

CHARACTERS :

Anterior fin completely rayed, rounded, begins slightly behind the ventral ganglion. Length 10–19% of body length.

Posterior fin rounded.

Tail slender, 20–28% of body length.

Anterior teeth up to 8, usually 6–7 (see Text-fig. 4).

Posterior teeth up to 17, usually 14–15 (see Text-fig. 4).

Hooks 7 to 11, usually 8–9 (see Text-fig. 4).

Seminal vesicles conical, very close to tail fin (see Plate 1b, fig. 5a).

Ovaries observed up to ventral ganglion.

Collarette prominent between head and anterior fins, but very thin on remainder of the body.

Corona commences at the posterior end of the head and reaches about $\frac{1}{3}$ of the distance to the ventral ganglion (see Text-fig. 5b).

Length up to 28.5 mm.

Distribution Probably a purely Antarctic form, extending from the surface down to about 1,500 m., though commonest between 750 and 250 m. Breeds in deep water.

DISCUSSION

Although as already mentioned it is easy to separate *S. planctonis* Steinhaus and *S. zetesios* Fowler from *S. marri* by the shape and position of the seminal vesicles, these structures are seldom visible in the first two mentioned species (see p.437). In *S. marri* however traces of the vesicles are visible in animals as small as 12 mm. long, while no trace of a vesicle is normally visible in specimens of the other two species less than 25 mm. long. Something more is therefore needed to differentiate them when immature, and in Text-fig. 6 I have been able to show how the length of the anterior fin expressed as a percentage of the total length can be used to do so. It will be seen that this percentage is less than 20 in *S. marri*, more than 20 in *S. zetesios* and 24 or more in *S. planctonis*. As far as the two latter species are concerned however the amount of overlap is perhaps too great for this feature to be of diagnostic value except where large numbers of specimens are involved.

These percentage differences apart, the shape and structure of the anterior fins are of some taxonomic importance. In *S. marri*, as Text-fig. 3 shows, they are regularly arcuate, having their greatest width at the middle, and are completely rayed. In both *S. planctonis* and *S. zetesios* they are elongate, widest at the posterior end and either rayless or having only a few widely spaced rays in front.

Although *S. planctonis* and *S. zetesios* cannot usually be distinguished by differences in the ratio of anterior fin length to body length, the posterior teeth if plotted against the body length (Text-figs. 2 and 7) demonstrate how readily distinguishable, in their older stages at any rate, they can be. Fig. 2 has been compiled from the work of earlier authors. It includes all available previous records of *S. planctonis*, records of *S. zetesios* by Fowler (1905, 1906) and records of *S. planctonis* (= *S. zetesios*), "90 specimens from the Atlantic Ocean" by Ritter-Zahony (1911, p. 30). Taking all sizes above 15 mm. it will be seen from this figure that only in one instance, a record by Ritter-Zahony of a specimen of *S. planctonis* (= *S. zetesios*) 20 mm. long with only 12 posterior teeth, do the two sets of data overlap. The records of Thomson (1947) for *S. planctonis*, which were given for 5 mm. size groups, have been plotted in the middle of each such size group. Text-fig. 7 has been compiled from "Discovery" data. It confirms the previous work on *S. zetesios*, apart from the one anomalous Ritter-Zahony record, and amplifies the previous work on *S. planctonis*. In this figure the data plotted were from specimens from a large number of plankton samples in the "Discovery" collections, selected so as to cover as much of the size range of the species as possible. The samples were collected at depths from the surface to 2000 m. in the North and South Atlantic Oceans, the Tasman Sea, the Indian and South Pacific Oceans at different seasons of the year. The data shown in the

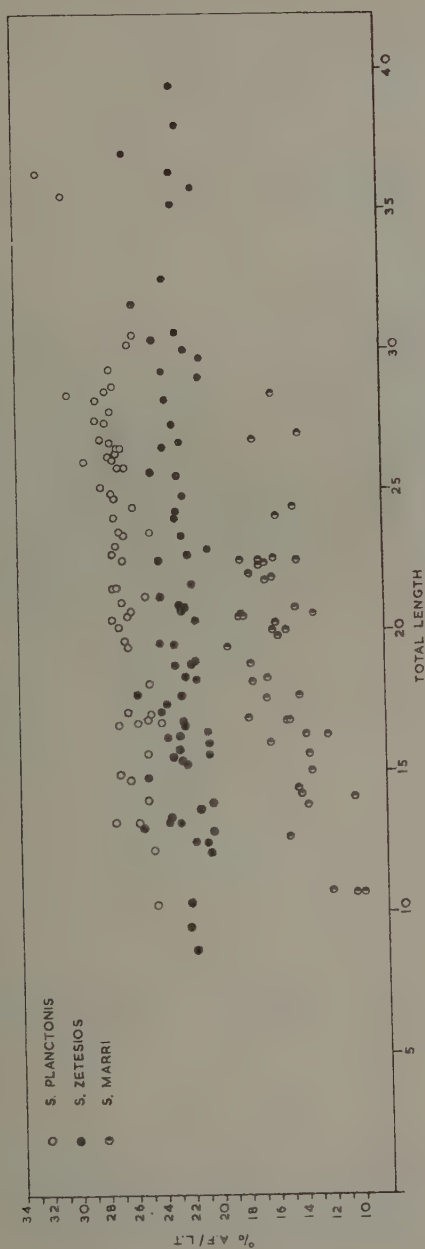


FIG. 6.—Ratio anterior fin length to body length plotted against body length.

figure can therefore be taken to cover seasonal and distributional variations, if any, though the sample is not a fair one for statistical purposes.

It is evident then that above 15 mm. specimens of *S. planctonis* and *S. zetesios* can readily be distinguished by their posterior teeth numbers and that below this size these numbers more or less overlap and would not be a reliable distinguishing feature. I have been unable to find a method of distinguishing them below this size, and the small specimens in Text-figs. 2 and 7 have been identified only by being present in hauls which apparently contained but one species. This is not altogether satisfactory and it is hoped that further work may produce a reliable method of identifying the young forms.

Distributional evidence shows that *S. zetesios* is a typically mesoplanctonic form, while records of *S. planctonis*, although scarce, all point to its being epiplanktonic. The species described by Moore (1949) from the surface waters round Bermuda is almost certainly *S. planctonis* although he gives no counts of posterior teeth to confirm it. Steinhaus's records were from shallow hauls as also were those of Tokioka (1940). Thomson (1947) gives the vertical distribution as abundant between 0 and 100 m., and numerous down to 500 m. *S. planctonis* has been taken in shallow hauls at various "Discovery" stations e.g. 1608.—36° 07' S., 22° 53·8' E., 10.xi.35. 1609.—37° 08·4' S., 27° 03·1' E., 11.xi.35. 1610.—38° 31·9' S., 31° 11·5' E., 12.xi.35. 2729.—35° 37' S., 160° 22' E., 21-22.x.50. 2730.—35° 58' S., 163° 39' E., 22.x.50. 2734.—45° 00' S., 173° 39' W., 5-6.xi.50. 2920.—48° 45' N., 18° 52' W., 4.vi.52.

KEY

S. planctonis group

Robust chaetognaths; usually opaque and white when preserved, having an extensive collarette which in well preserved specimens extends to the tail, and in all specimens to the anterior fins.

- | | | | | | | |
|--|---|---|---|---|---|----------------------|
| 1. Length of anterior fin more than 20% of total body length | . | . | . | . | . | 2 |
| Length of anterior fin less than 20% of total body length | . | . | . | . | . | <i>S. marri</i> |
| 2. Posterior teeth usually more than 14*, deep water form | . | . | . | . | . | <i>S. zetesios</i> |
| Posterior teeth usually less than 14*, shallow water form | . | . | . | . | . | <i>S. planctonis</i> |

* See Text-fig. 7.

ACKNOWLEDGMENTS

I would like to thank Mr. J. W. S. Marr for a great deal of advice and assistance, and Dr. J. H. Fraser, F.R.S.E. for reading the typescript.

SUMMARY

Specific distinction between *S. planctonis* and *S. zetesios*, on the one hand, and *S. marri*, on the other, depends primarily on the shape and position of the seminal vesicles; three other features, the shape of the fins, the length of the anterior fins, and the total length at maturity provide additional diagnostic characters. By the use of these points *S. marri* can be distinguished at all sizes above about 8 mm.

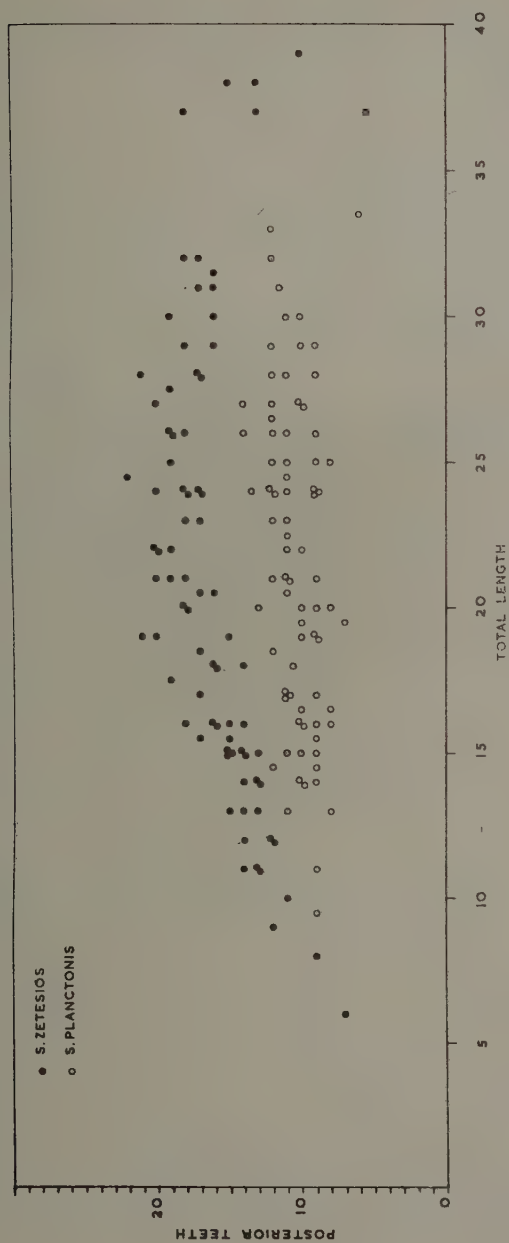


FIG. 7.—The mean of the sum of each pair of posterior teeth plotted against body length for *S. planctonis* and *S. zetesios*. Data from "Discovery" collections, from many stations in different localities at different seasons.

The separation of *S. planctonis* and *S. zetesios* is less satisfactory and rests upon the numbers of posterior teeth in animals over 15 mm. in length which is the only observed taxonomic difference. It is probable that depth distribution will provide further supporting evidence for the existence of these two undoubtedly separate species, but this has yet to be fully worked out.

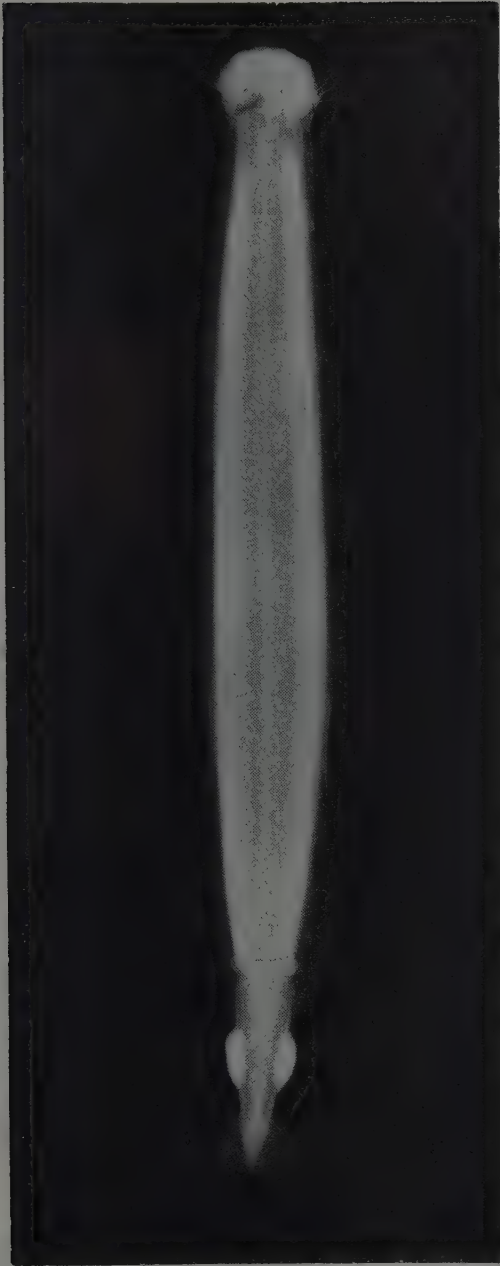
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PLATE II

- (a) *Sagitta planctonis* Steinhaus. A fully mature specimen 37 mm. long.
(b) *Sagitta marri* nov. sp. A mature specimen 28 mm. long.



a



b

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VOL IV
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